Residual feed intake adjusted for backfat thickness and feeding frequency is independent of fertility in beef heifers

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Abbreviations: ADG, average daily gain; **DMI**, dry matter intake; **FCR**, feed conversion ratio; **ME**, metabolizable energy; **RFI_{fat}**, residual feed intake adjusted for off-test ultrasound backfat thickness; **$RFI_{fat\ \&\ activity}$**, residual feed intake adjusted for off-test backfat thickness and feeding event frequency

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ABSTRACT

Basarab, J. A., Colazo, M. G., Ambrose, D. J., Novak, S., McCartney, D. and Baron, V. S. 2011. **Residual feed intake adjusted for backfat thickness and feeding frequency is independent of fertility in beef heifers**. Can. J. Anim. Sci. **91**: 573–584. This study examined the effects of residual feed intake (RFI), RFI adjusted for off-test backfat thickness (RFI_{fat}) and RFI adjusted for off-test backfat thickness and feeding event frequency ($RFI_{fat\ \&\ activity}$) on heifer fertility and productivity. Beef heifers (n=190) were monitored for individual daily feed intake and feeding event activity over 108–112 d using the GrowSafe System® and assessed for age at puberty based on plasma progesterone concentration. Individual animal daily feed intake, feeding event activity and off-test backfat thickness were then used to calculate RFI, RFI_{fat} and $RFI_{fat\ \&\ activity}$ and group heifers as either negative ([−], RFI<0.0) or positive ([+], RFI≥0.0) for RFI. Heifers averaged 298 kg (SD=34) in body weight, were 276 days of age (SD=19) at the start of test, grew at 0.90 kg d^{-1}(SD=0.21), consumed 7.62 kg DM $head^{-1}$ d^{-1} (SD=0.84) and had a feed conversion ratio of 8.93 (SD=2.43). Age (351 d, SD=43) and weight (367.3 kg, SD=45.0) at puberty were similar between [−] and [+] RFI heifers, but age at puberty was delayed in [−] RFI_{fat} (P=0.04) and $RFI_{fat\ \&\ activity}$(P=0.08) heifers compared with [+] RFI_{fat} and $RFI_{fat\ \&\ activity}$ heifers. Efficient or [−] RFI heifer exhibited a lower pregnancy (76.84 vs. 86.32%, P=0.09) and calving rate (72.63 vs. 84.21%, P=0.05) compared with [+] RFI heifers. These differences were partially removed in [−] RFI_{fat} and completely removed in [−] $RFI_{fat\ \&\ activity}$ compared with their [+] RFI counterparts (pregnancy rate, 80.85 vs. 82.29%, P=0.80; calving rate, 75.53 vs. 81.25%, P=0.34). No differences were observed between efficient and inefficient heifers in calving difficulty, average calving date, age at first calving, calf birth weight, calf pre-weaning ADG, calf weaning weight and heifer productivity. However, [+] RFI heifers exhibited a 1.9-fold higher calf death loss compared with [−] RFI heifers (11.11% vs. 5.71%, P=0.24). This difference was more pronounced in [+]

RFI_{fat} and [+] $RFI_{fat\ \&activity}$ heifers, which exhibited 2.2-fold (11.84% vs. 5.33%, P=0.15) and 3.0-fold (12.66% vs. 4.17%, P=0.06) higher calf death loss compared with [−] RFI heifers. There was no relationship of RFI adjusted for backfat thickness and feeding activity on fertility traits indicating that backfat thickness and feeding activity may be associated with feed intake and should be considered when selecting heifers for improved feed efficiency.

Keywords: Beef heifer, age at puberty, feeding behaviour, fertility, productivity

Feed costs are a severe and growing challenge to the global competitiveness and sustainability of beef production, and 56–71% of the cost of cow-calf production was associated with feed, bedding and pasture (Alberta Agriculture and Rural Development 2005). Feed energy for cow maintenance represents 65–75% of total feed energy requirements (Ferrell and Jenkins 1985; Montano-Bermudez et al. 1990), with considerable individual animal variation independent of body size and growth (Arthur et al. 2001a, b; Basarab et al. 2003; Crews 2005). In the past, feed conversion ratio (FCR) has been used for improving feed efficiency; however, it has been ineffective since FCR is related to growth, body size and body composition (Archer et al. 1999; Johnson et al. 2003; Crews 2005). Alternatively, residual feed intake (RFI) has become a preferred method of improving feed efficiency in beef cattle as it is independent of body weight and average daily gain (Archer et al. 1997; Basarab et al. 2003; Nkrumah et al. 2007). Presently innovative seedstock producers are rapidly increasing their capacity to measure young bulls for feed intake and RFI, and to develop estimated breeding values and multi-trait selection indices that produce feeder progeny that perform profitably in the feedlot and give optimum carcass quality (Crews et al. 2006; Carstens and Tedeschi 2006). Replacement heifers are also being selected from low RFI bulls or from heifers measured directly for RFI with only a limited understanding of its effects on herd fertility. In addition, young bulls and heifers are usually tested for RFI between 7 and 12 mo of age when they are at different stages of sexual maturity, such that some animals will have reached puberty at the start of the feed intake test period (early maturing) while others will not reach puberty until after the test period has ended (late maturing). This testing approach may favor the selection of slightly later maturing animals (Arthur et al. 2005; Basarab et al. 2007; Basarab et al. 2009) possibly leading to herd infertility since early maturing heifers and bulls may consume more feed energy during the test period due to sexual development and activity than late maturing animals given equal age, body weight, growth rate and body composition (National Research Council [NRC] 1996). These authors suggested that this difference was due to delayed puberty and conception in heifers, which was then maintained with no further reductions in fertility throughout the cow's lifetime. Thus, the objectives of this study are (1) to examine the effects of RFI on age at puberty, age at conception, pregnancy rate and productivity in heifers, and (2) to identify variables that would adjust RFI to be independent of heifer fertility and productivity.

MATERIALS AND METHODS

All animals were maintained at the Agriculture and Agri-Food Canada Lacombe Research Centre and were cared for according to the guidelines of the Canadian Council on Animal Care (1993). The management of the cow-calf herd has previously been described by Basarab et al. (2007), with the exception that all bred heifers are vaccinated 6 wk pre-calving as an aid in preventing diarrhoea in their calves caused by bovine rotavirus (serotypes G6 and G10), bovine coronavirus, enterotoxigenic strains of *Escherichia coli* having the K99 pili adherence factor, and *Clostridium perfringens* type C. Bred heifers are then re-vaccination at 4 to 5 wk before the busiest week of the calving season (usually week 2). Growth promoting implants were not used in this study.

In October of 2006, 2007 and 2008, heifers were weaned and 30–50% were selected as herd replacements based on body weight, frame size, temperament, mother's lifetime productivity and mother's udder conformation (61 in 2006; 68 in 2007; 61 in 2008). At weaning these 190 heifers averaged 179 d of age (SD=12 d) with a range in age from 144 to 206 d, and were 244.0 kg in body weight (SD=23.7 kg). They consisted of 116 Aberdeen Angus-Hereford (ANHE) and 74 Charolais-Red Angus-Maine Anjou (CHARMA) crossbred heifers. The 2006 born ANHE heifers were produced from Hereford sires whereas the CHARMA heifers were produced from Red Angus sires. The 2007 and 2008 born ANHE heifers were produced from Hereford and Aberdeen Angus bulls and the CHARMA heifers were produced from Charolais sires. This resulted in a breed composition of 66.4% Aberdeen Angus and 33.6% Hereford for ANHE heifers, and 57.1% Charolais, 21.9% Red Angus, 10.5% Maine Anjou and 10.5% other breeds (Hereford, Aberdeen Angus and Simmental) for CHARMA heifers. The heifers were placed into a feedlot pen and fed barley silage once daily from weaning to the beginning of the pre-test adjustment period (2–3 mo). Heifers were then moved to a feedlot pen (86 m by 46 m; 65 m^2 per animal) fitted with 16 GrowSafe® (GrowSafe Systems Ltd., Airdrie, AB) feeding stations for the automatic monitoring of individual animal feed intake and feeding behaviours, where they were adjusted to a 90% barley silage plus 10% rolled barley grain diet, fed twice daily ad libitum over the next 28–35 d. The adjustment period was followed by a 108- to 113-d test. The diet was chosen as it reflects feeds readily available in central Alberta and is typical for replacement heifer where weight gains of 0.75 to 0.9 kg $d^{-1}$are targeted. Heifers had free choice access to fresh water, salt and a mineral plus vitamins premix (FEED-RITE RITE-MINS BEEF COW CALVING PLUS MINERAL, Feed Rite, A Division of Ridley Inc., 34 Terracon Place, Winnipeg, MB, Canada R2J 4G7) throughout all aspects of the study. They were weighed on 2 consecutive days at the start and end of the test period, and at approximately 28-d intervals. Heifers were also measured for ultrasound backfat thickness (mm), longissimus thoracis area (cm^2) and marbling score at the start and end of the test period. Marbling score is a measure of intramuscular fat where trace marbling or less=1.00 to 3.99 (Canada A quality grade), slight marbling=4.00 to 4.99 (Canada AA quality grade), small to moderate marbling=5.00 to 7.99 (Canada AAA quality grade) and slightly abundant or more marbling=8.00 to 11.00 (Canada Prime). Ultrasound measurements were taken with an Aloka 500V diagnostic real-time ultrasound with a 17-cm 3.5 Mhz linear array transducer (Overseas Monitor Corporation Ltd., Richmond, BC) by a certified ultrasound technician using procedures described by Brethour (1992). The GrowSafe® feeding stations and concrete apron were covered by an open-sided wooden roof that prevented precipitation from entering the feeding stations. Wood chips and shavings were used as bedding and were placed into the pen as required. The methodology for measuring feed intake (kg DM d^{-1}) and feeding behaviours (daily feeding event frequency, duration [min d^{-1}] and head-down time [min d^{-1}]) using the GrowSafe® System has been described by Basarab et al. (2003, 2007).

Feed samples of the total mixed ration for the heifers were collected weekly, pooled monthly and analysed for dry matter, calcium, phosphorus, crude protein, neutral detergent fibre and acid detergent fibre. Dry matter was determined by drying a sample of the diet at 100^{o}C in a forced-air oven to a constant weight. The calcium (AOAC Official Method 927.02) and phosphorus (AOAC Official Method 946.06) contents of the samples were determined by AOAC procedures (AOAC 1996). Crude protein was calculated as 6.25×N (AOAC 1996, Official Method 973.03). Neutral detergent fibre and acid detergent fibre contents of feed were determined by the procedure of Van Soest et al. (1991).

Plasma Progesterone Concentrations

Blood samples were collected by jugular venipuncture on the first day of test in 2007, 35 d before the start of the test in 2008, and 57 d before the start of the test in 2009 and at 8- to 11-d intervals each year for determining puberty based on progesterone concentrations. Total blood collection period spanned 122, 157 and 151 d in 2007, 2008 and 2009, respectively. Samples collected into evacuated tubes containing sodium heparin (Vacutainer, Beckton Dickinson and Co., Franklin Lakes, NJ) were immediately placed on ice and centrifuged within 3 h at 4°C for 20 min at 1500×*g*. Plasma was separated and stored at −20°C until progesterone concentrations were determined. Progesterone concentrations were determined, in duplicate, using a commercially available RIA kit (Coat-A-Count Progesterone; Diagnostic Products Corporation, Los Angeles, CA) as previously described by Colazo et al. (2008). The sensitivity of this assay is 0.1 ng mL^{-1}. The intra- and inter-assay coefficients of variations were 2.6 and 17.2%, respectively. Heifers were considered to have reached puberty when the concentration of progesterone in the plasma samples was ≥1 ng mL^{-1} (Ringuet et al. 1994).

Pre- and Post-Breeding Period

The feed intake test ended in May and breeding started the first week in June of each year. Heifers were moved to a meadow-brome grass (*Bromus riparius* Rehm.) alfalfa (*Medicago sativa* L.) pasture and exposed to natural service (15:1 heifer to bull ratio) over a 37-d breeding season. Transrectal ultrasonography (Aloka SSD 500 attached to a 7.5 MHz linear-array transducer) was used to assess ovarian structures and to determine abnormalities of the reproductive tract 1 wk prior to the start of breeding, and also to determine pregnancy status 1 mo following the end of breeding. The age of the conceptus was determined as previously described by Curran et al. (1986) and reported in 5-d increments.

Calculations

Heifer on-test body weight, mid-point weight and average daily gain (ADG) were calculated by a linear regression of the animal's observed body weight against day on-test (Basarab et al. 2003; Wang et al. 2006). Average daily feed intake of each heifer over the test period was converted to total dry matter intake (DMI) and then converted to total metabolizable energy (ME) intake based on the DM and ME content of the diet given in Table 1. Diet ME content was calculated as follows: Total digestible nutrients, TDN (%)=96.03 − [1.034×ADF,%], where ADF refers to acid detergent fibre given in Table 1 (Norwest Laboratories, 3131-1 Ave. South, Lethbridge, AB, Canada T1J 4H1). ME, MJ kg^{-1} DM diet=((% TDN/100)×4.4 Mcal kg^{-1} TDN)×4.184 MJ DE $Mcal^{-1}$×0.82 MJ ME MJ^{-1} DE (NRC 1996). Total ME consumption of each animal was then divided by 10 to give total DMI standardized to an energy density of 10 MJ ME kg^{-1} DM, thus making the results comparable with other research findings previously reported (Arthur et al. 2001a; Basarab et al. 2003; Nkrumah et al. 2006). Total standardized DMI was then divided by the number of days on test to give average standardized daily DMI (SDMI, kg DM d^{-1}). The SDMI of each animal within contemporary group was then regressed against ADG (kg d^{-1}) and metabolic MIDWT ($kg^{0.75}$) using PROC GLM (SAS Institute, Inc. 2009) and the following model:

$$\text{Model 1: } Y_{ij} = \beta_0 + \beta_1 \text{ADG}_i + \beta_2 \text{metabolic MIDWT}_j + e_{ij},$$

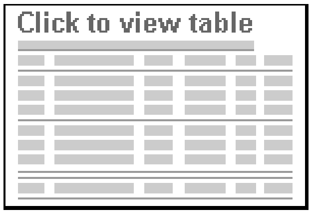

Table 1. Composition of diet fed to replacement heifers by test year

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where Y_{ij} is the SDMI for animal ij, β_0 is the regression intercept, β_1 is the partial regression coefficient of SDMI on average daily gain, β_2 is the partial regression coefficient of SDMI on metabolic mid-weight, and e_{ij} is the random error term. A second and third model were developed that adjusted RFI for backfat thickness, and backfat thickness and feeding activity in an effort to remove effects of sexual development and activity on feed intake and were as follows:

$$\text{Model 2: } Y_{ijk} = \beta_0 + \beta_1 \text{ADG}_i + \beta_2 \text{metabolic MIDWT}_j + \beta_3 \text{BFend}_k + e_{ijk},$$

where β_3 is tye partial regression coefficient of SDMI on final ultrasound back fat thickness (mm).

$$\text{Model 3: } Y_{ijk1} = \beta_0 + \beta_1 \text{ADG}_i + \beta_2 \text{metabolic MIDWT}_j + \beta_3 \text{BFend}_k + \beta_4 \text{ACTIVITY}_1 + e_{ijk1},$$

where β_4 is the partial regression coefficient of SDMI on average feeding event frequency (events d^{-1}). Residual feed intake, unadjusted (RFI) and adjusted for backfat thickness (RFI_{fat}) and feeding event frequency ($RFI_{fat\ \&\ activity}$) were then computed for each animal as the deviation of SDMI from the expected feed intake ([EFI]; RFI=SDMI – EFI_I), SDMI from EFI_{II} (RFI_{fat}=SDMI – EFI_{II}) and SDMI from EFI_{III} ($RFI_{fat\ \&\ activity}$=SDMI – EFI_{III}). RFI, RFI_{fat} and $RFI_{fat\ \&\ activity}$ were then each used to group heifers as either negative (RFI<0.0) or positive (RFI ≥ 0.0) for RFI. This method was selected to maximize the number of observations for each RFI grouping. Weight at puberty was determined as follows: ([date at puberty – on-test start date]×on-test ADG, kg d^{-1})+on-test start weight (kg). Heifer productivity, expressed as kilograms calf weaned per heifer exposed to breeding, was calculated as follows: Heifer productivity (kg calf weaned per heifer exposed to breeding)=(calf pre-weaning ADG, kg d^{-1}×calf gender adjustment factor×calf age at weaning, d)+(calf birth weight, kg×calf gender adjustment factor), where calf gender adjustment factor was 1.08 for heifers and 1.00 for steers since 200-d weaning weight for steers was 8% more than for heifers (242.8 kg vs. 224.7 kg). Heifers that were open or that did not wean a calf were given a productivity of zero.

Dystocia score, presentation type (normal; abnormal), birth type (single; twin) and calf condition score were assigned within 24 h of birth. Dystocia score ranged from 1 to 4, where 1 is unassisted, 2 is easy pull, 3 is hard pull (calf puller), and 4 is Caesarean section was used. Dystocia scores were later collapsed into two groups: dystocia scores 1 and 2 represented easy births and 3 and 4 represented difficult births. This was done because dystocia scores 3 and 4 are of economic importance to cow-calf managers (Basarab et al. 1993). Calf condition score ranged from 1 to 6, where 1 is born alive and healthy, 2 is died after weaning, 3 is died after branding at 2 mo of age or older, 4 is died before 2 mo of age, 5 is dead at birth and 6 is aborted. The actual date of death and reason (if possible) were also recorded.

Statistical Analysis

With the exception of birth date and ages, pre-calving heifer traits and heifer productivity (kilograms calf weaned per heifer exposed to the bull) were subjected to an analysis of covariance using PROC MIXED (SAS Institute, Inc. 2009) and the following model:

$$Y_{ijkl} = \mu + Y_i + B_j + YB_{ij} + R_k + YR_{ik} + BR_{jk} + YBR_{ijk} + \beta_1 \mathrm{BIRTH}_l + e_{ijkl},$$

where Y_{ijkl} is the individual animal observation, Y_i is the effect of the ith year or contemporary groups (2007, 2008, 2009), B_j is the effect of the jth breed cross (ANHE; CHARMA), R_k is the effect of the kth heifer RFI, RFI_{fat} and $\mathrm{RFI}_{fat\ \&\ activity}$ groups, YB_{ij}, YR_{ik}, BR_{jk} and YBR_{ijk} are the two- and three-way interaction terms, β_1 is the partial regression coefficient of heifer birth date (BIRTH) and e_{ijkl} is the random error. Heifer birth date and ages were analyzed similarly, except that heifer birth date was not included in the statistical model. Post-calving heifer traits were also subjected to an analysis of covariance using PROC MIXED (SAS Institute, Inc. 2009), but with the following model:

$$Y_{ijklm} = \mu + Y_i + B_j + YB_{ij} + R_k + YR_{ik} + BR_{jk} + YBR_{ijk} + S_l + YS_{il} + BS_{jl} + RS_{kl} + YBS_{ijl} + YRS_{ikl} + BRS_{jkl} + YBRS_{ijkl} + \beta_1 \mathrm{BIRTH}_m + e_{ijklm},$$

where Y_{ijklm} is the individual animal observation, S_l is the effect of the lth calf gender, YS_{il}, BS_{jl}, RS_{kl}, YBS_{ijl}, YRS_{ikl}, BRS_{jkl} and $YBRS_{ijkl}$ are the two- three and four-way interaction terms with calf gender and e_{ijklm} is the random error. A further analysis was conducted to determine the DMI and feed efficiency associated with sexual development and activity. This was accomplished by identifying when heifers reached puberty relative to the start of the feed intake test period. Heifers were then identified as pre-pubertal during 0 to 84 d on test or post-pubertal from 42 to 113 d on test. The numbers of days for each puberty status (pre-pubertal, 0–84 d vs. post-pubertal, 42–113 d) were selected to obtain the maximum number of feed intake days for each puberty status. The average daily feed intake for each heifer within puberty status (84 d for pre-pubertal; 71 d for post-pubertal) were then re-calculated, along with a new mid-point weight (mid-point weight equals day 42 for pre-pubertal and day 77.5 for post-pubertal heifers). Feed intake and FCR data were then subjected to an analysis of covariance using PROC MIXED (SAS Institute, Inc. 2009) and the following model:

$$Y_{ijklm} = \mu + Y_i + B_j + YB_{ij} + P_k + YP_{ik} + BP_{jk} + YBP_{ijk} + \beta_1 \mathrm{ADG}_l + \beta_2 \mathrm{PUBMIDWT}_m + \beta_3 \mathrm{BFend}_n + e_{ijklmn},$$

where Y_{ijklmn} is the individual animal observation, P_k is the effect of the kth puberty status, YP_{ik}, $BP_{jk}$and YBP_{ijk} are the two- and three-way interaction terms with puberty status, β_1 is the partial regression coefficient of DMI or FCR on ADG, β_2 is the partial regression coefficient of DMI or FCR on midpoint weight for pre- or post-pubertal heifers, β_3 is the partial regression coefficient of DMI or FCR on final off test backfat thickness and e_{ijklmn} is the random error. Within animal, the overall ADG equalled their puberty status ADG, since growth was linear over the entire test period. Those sources of variation with significant ($P<0.05$) F values were subjected to multiple comparisons of least squares means using the PDIFF option of the SAS Institute, Inc. (2009). Simple correlations were computed using PROC CORR of the SAS Institute, Inc. (2009). Differences among [–] and [+] RFI, RFI_{fat} and $\mathrm{RFI}_{fat\ \&\ activity}$ heifers for age at puberty, pregnancy rate, calving pattern, calving difficulty, weaning rate and calf death loss were analyzed with the PROC FREQ procedure of SAS using the CHISQ option (SAS Institute, Inc. 2009).

RESULTS AND DISCUSSION

Data quality parameters for individual animal growth curves and feed intake data are given in Table 2. Heifers ranged in age at the start of test from 229 to 286 d in 2007, from 232 to 289 d in 2008 and from 272 to 314 d in 2009, and these values were within the start of test age range of 60 d recommended by the Beef Improvement Federation guidelines (BIF 2010). Length of test (108 to 113 d) and recorded live weight at 28-d intervals were also considered adequate to accurately compute ADG and average daily feed intake for individual animals (Wang et al. 2006; BIF 2010). Mean assigned feed disappearance within year was greater than 98% and only 0.9 to 3.1% of data were removed due to system malfunction, power outage and non-detection of consumed feed. The moderate to high correlations of DMI on ADG and DMI on body size are also indicative of high data quality. All growth curves had a coefficient of determination (R^2×100) greater than 95% (mean=98.2%, SD=1.7), indicating that all animals grew normally, without hindrance from morbidity or nutritional restrictions. The high R^2 values also indicated that growth during this phase of the animal's life was linear and that the choice of a linear regression model was appropriate. The RFI component traits of ADG and metabolic mid-weight also accounted for a significant proportion of the variation in DMI (67.3 to 79.8%), which is consistent with other studies (Arthur et al. 2001a, b; Basarab et al. 2003, 2007; Nkrumah et al. 2007; Kelly et al. 2010a, Kelly et al. 2010b). The inclusion of final off-test backfat thickness into the regression model accounted for an additional 0.3–3.8% of the variation in DMI (P<0.05) and the inclusion of feeding event frequency accounted for a further 0.9–3.5% (P<0.05) of the variation in DMI over that accounted for by ADG, metabolic mid-weight and final off-test backfat thickness.

»View table **Table 2.** Mean and standard deviations [z] for data quality parameters for average daily gain (ADG) and feed intake by year on test

The least squares means of growth, body composition, feeding behaviour and feed efficiency traits for [−] and [+] RFI heifers are given in Table 3. Heifer birth date and weight, weaning age and weight, weight on- and off-test, l. thoracis area on- and off-test, growth rate, mid-point metabolic weight and two of three feeding behaviour traits were similar between [−] and [+] RFI, RFI_{fat} and $RFI_{fat\ \&\ activity}$ heifers. Notable exceptions were on-test-marbling score, off-test backfat thickness and feeding event frequency, with [−] RFI heifers carrying 3.2% less intramuscular and 6.8% less subcutaneous fat, and feeding 6.8% less frequently than [+] RFI heifers. There were no differences in body fatness between [−] and [+] RFI_{fat}heifers, nor in body fatness and feeding event behaviours between [−] and [+] $RFI_{fat\ \&\ activity}$ heifers, since these RFI values had been adjusted for these component traits. As expected, [−] RFI, RFI_{fat} and $RFI_{fat\ \&\ activity}$ heifers consumed 7.1, 6.1, and 5.4% less feed than [+] RFI, RFI_{fat} and $RFI_{fat\ \&\ activity}$heifers, respectively, which resulted in a 6.4 to 7.6% improvement in feed conversion ratio in efficient heifers. These results are similar to those reported previously by Canadian (Basarab et al. 2003, 2007; Nkrumah et al. 2007), Australian (Arthur et al. 2001a, b; Richardson et al. 2001), American (Carstens and Tedeschi 2006) and Irish (Kelly et al. 2010a, Kelly et al. 2010b) researchers who reported moderate to high positive relationships of RFI on DMI (r_p=0.60 to 0.72; r_g=0.69 to 0.79) and RFI on FCR (r_p=0.53 to 0.70; r_g=0.66 to 0.88). In the present study, all three measures of RFI were highly related (r_p=0.92–0.96; P<0.001) indicating that they are similar traits.

»View table **Table 3.** Growth, body composition and feed efficiency traits for [−] and[+] residual feed intake heifers during their post-weaning test period

Only 9.0% of heifers had reached puberty by the start of the feed intake test, while 27.5% had not reach puberty by the end of the feed intake test (Fig. 1). The percentages of heifers reaching puberty during days 0, 14, 28, 42, 56, 70, 84, 98 and 112 of the test period were 9.0, 11.1, 19.6, 22.2, 27.5, 42.9, 60.3, 70.4 and 72.5%, respectively. This resulted in heifers reaching puberty at various times during the test period with varying energy demands due to sexual activity and development. Figure 1 shows that heifers that had attained puberty near the start or within 30–60 d after the test started consumed more feed (r_p=−0.19), spent more time at the bunk in feeding event duration (r_p=−0.13) and head-down (r_p=−0.23) behaviours, but removed their head from the bunk or went to the bunk less frequently (r_p=0.15) than heifers reaching puberty near the end of the test or after the test had finished. In the present study heifers group as pre-pubertal (n=109) consumed 4.7% less feed (7.47±0.04 vs. 7.84±0.06 kg DM d^{-1}, P<0.001) and had a 7.4% improvement in FCR (8.65±0.07 vs. 9.34±0.09 kg DM kg^{-1} gain, P<0.001) compared with heifers grouped as post-pubertal (n=81) given equal ADG, body size and backfat thickness. While no other data are available to directly show the added energy demand of sexual development and activity it is assumed that there will be a cost since cattle require 14.4% more energy when standing than when lying (Susenbeth et al. 2004), and Richardson et al. (1999) reported a positive correlation (r=0.32) between daily pedometer count and DMI. In addition meta-analysis of 18 research trials reported that feeding melengestrol acetate, an oestrus suppressant, to non-implanted feedlot heifers improved (P<0.01) feed efficiency by 4.4% (Wagner et al. 2007). Thus, these results suggest that calculating RFI from a mixture of pre- and post-pubertal heifers will favor later-maturing heifers since they have an estimated 4–7% lower feed efficiency given equal growth, body size and body composition.

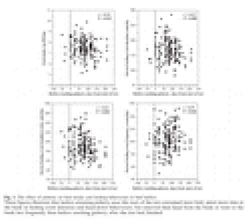

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Fig. 1. The effect of puberty on feed intake and feeding behaviours in beef heifers. These figures illustrate that heifers attaining puberty near the start of the test consumed more feed, spent more time at the bunk in feeding event duration and head-down behaviours, but removed their head from the bunk or went to the bunk less frequently than heifers reaching puberty after the test had finished.

Age and weight at puberty for all heifers averaged 351 d and 367 kg, respectively, and age at puberty ranged from 243 to 441 d (Table 4). This average weight at puberty represented 56.5% of mature weight since pre-breeding body weight of mature cows in this herd was previously reported to be 649 kg (Basarab et al. 2007). Martin et al. (2007) reported similar results for spring-born Angus×Simmental, Angus×Gelbvieh and MARC III (¼ Angus, ¼ Hereford, ¼ Red Poll, ¼ Pinzgauer)×Red Angus heifers grown at 0.60–0.65 kg d^{-1} for the 6.5 mo period prior to the beginning of the breeding season. In their study age and weight at puberty were 353 d and 315 kg, respectively. Almost four decades ago average age at puberty in British×British and British×Continental heifers were 350–370 d, while average weight at puberty ranged from 270 to 340 kg (Laster et al. 1972).

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Table 4. Age and weight at puberty in [−] and [+] residual feed intake (RFI, RFI_{fat} and $RFI_{fat\ \&\ activity}$) replacement heifers

There was no difference between [−] and [+] RFI heifers in age at puberty, weight at puberty or the rate at which heifers reached puberty (Table 4). Ninety-seven percent (97%) of heifers, regardless of RFI group or method of calculating RFI, reached puberty by 15 mo of age, which is required if they are to calve by 24 mo of age. When RFI was adjusted for final ultrasound backfat thickness and feeding event frequency, [−] RFI_{fat} and $RFI_{fat\ \&\ activity}$ heifers took 11 and 13 d longer to reach puberty and were 12.1 and 14.5 kg heavier than [+] RFI_{fat} and $RFI_{fat\ \&\ activity}$, respectively. This was reflected in the rate at which heifer's reached puberty with [−] RFI_{fat} and $RFI_{fat\ \&\ activity}$ heifers having a lower proportion reaching puberty by 9 mo of age compared with [+] RFI_{fat} and $RFI_{fat\ \&\ activity}$ heifers. Our results are similar to Shaffer et al. (2011) who reported a small but negative linear relationship between RFI and age at puberty (r=−0.16, P=0.06), such that for each unit increase in RFI there was a corresponding reduction of 7.5 d in age at puberty. Their study was conducted with pre-pubertal heifers that reached puberty during the course of the feed intake test period. These researchers concluded that due to the large variation in age at puberty in both [−] and [+] RFI heifers, selection for low RFI and early maturing heifers would be highly possible, with minimal impact on herd fertility.

Pre- and post-breeding age and weight, abortion rate, heifer cull-death rate and average calving date for [−] and [+] RFI, RFI_{fat} and $RFI_{fat\ \&\ activity}$ heifers were similar (Table 5). However, [−] RFI heifers exhibited a lower rate of conception from days 12 to 37 of the breeding season, pregnancy rate (76.84 vs. 86.32%, P=0.092) and calving rate compared with [+] RFI heifers. When off-test backfat thickness was included in the model, [−] RFI_{fat} heifers still exhibited a lower rate of conception from day 22 to 32, but no difference in pregnancy rate compared with [+] RFI_{fat} heifers. When off-test backfat thickness and feeding event behaviour were included in the model, no differences were observed in rate of conception or pregnancy rate between [−] and [+] $RFI_{fat\ \&\ activity}$ heifers. These results suggest that selection for low RFI from a mixture of pre- and post-pubertal heifers can negatively impact fertility in [−] RFI heifers by favouring later-maturing heifers that do not yet have the extra energy demand associated with sexual development and activity. In addition, numerous studies have shown that RFI is positively related, both phenotypically and genetically, to body fatness (Arthur et al. 2001b; Richardson et al. 2001; Basarab et al. 2003; Nkrumah et al. 2004; Kelly et al. 2010a, Kelly et al. 2010b; Donoghue et al. 2011) such that [−] RFI heifer could have 2–5% less body fat than [+] RFI heifers, which may negatively impact the onset of puberty. However, all heifers in the present study had adequate nutrition as they grew at 0.90 kg d^{-1} and had 4.6 mm (range=1.4 to 8.5 mm) of ultrasound backfat thickness at the start and 5.9 mm (range=2.2 to 11.7 mm) at the end of the feed intake test. This level of backfat thickness equates to a body condition score of 2.5 to 3.0 (Basarab et al. 2007) based on the Scottish System (Lowman et al. 1976), where 1.0 is emaciated and 5.0 is grossly fat.

»View table **Table 5.** Pre- and post-breeding weight, pregnancy rate and calving rate in [−] and [+] residual feed intake (RFI, RFI_{fat} and $RFI_{fat\ \&\ activity}$) replacement heifers

Efficient or [−] RFI heifers also exhibited a slightly poorer performance by having fewer calves born by day 28 of the calving season than [+] RFI heifers (82.6% vs. 95.0%, P=0.02). This small delay in calving was removed by adjusting RFI for backfat thickness or backfat and average feeding event frequency. Only Arthur et al. (2005) has measured RFI in pre-pubertal heifers and then selected low RFI heifers as herd replacements. In that study no selection line differences were observed for pregnancy, calving and weaning rates. However, low RFI cows calved 5 d later (P=0.07) than high RFI cows. In a subsequent study, Basarab et al. (2007) reported that cows producing low RFI progeny calved 5–6 d later in the calving season (P<0.001) than dams that produced medium and high RFI progeny, and suggested that the effect was due to a delay in first oestrus resulting in a delay in conception during the breeding season. This Canadian study also reported no differences in pregnancy (95.6% vs. 96.0%; P=0.90), calving (84.9% vs. 86.3%; P=0.62) and weaning (81.5 vs. 82.3%, P=0.79) rates among cows that produced low or high RFI progeny.

Calving difficulty, age at first calving, calf birth weight, calf pre-weaning ADG, calf actual and 200-d weaning weight and heifer productivity, expressed as kilograms of calf weaned per heifer exposed to breeding, were similar between [−] and [+] RFI heifers regardless of RFI group or method used to calculated RFI (Table 6). This similarity in productivity occurred despite [−] RFI heifers having a lower pregnancy rate (76.84% vs. 86.32%, P=0.09) and resulted mainly because [−] RFI heifers also had a 1.9-fold lower (P=0.24) death loss of calves compared with [+] RFI heifers. This difference in calf death loss was more pronounced in [−] RFI_{fat} and [–] $RFI_{fat\ \&\ activity}$ heifers, which exhibited 2.2-fold (P=0.15) and 3.0-fold (P=0.06) lower death losses of calves compared with [+] RFI_{fat} and [+] $RFI_{fat\ \&\ activity}$ heifers, respectively. When calf death loss was adjusted to remove death loss due to known causes (calving difficulty; accidental, cow stepped on calf), [−] RFI, RFI_{fat} and $RFI_{fat\ \&\ activity}$ heifers had 2.6-fold (P=0.21), 3.0-fold (P=0.15) and 6.3-fold (P=0.04) fold lower death losses of calves compared with [+] RFI, RFI_{fat} and $RFI_{fat\ \&\ activity}$ heifers, respectively. Calf deaths that occur within 1 or 2 mo of birth and that are not due to calving difficulty or are not accidental may result because the calves are more susceptible to stress or may have suboptimal cellular immunity. Basarab et al. (2007) reported similar results in that cows that produced [+] RFI progeny also had nearly double the rate of calf death loss (8.06 vs. 4.24%, P=0.10) compared with cows producing [−] RFI progeny. In their study 85% of the calf death loss occurred before 2 mo of age and nearly half occurred near birth. The reason for the high baby calf death loss in [+] RFI cows and heifers is uncertain, though recent discoveries surrounding the physiological and biochemical mechanisms underlying low feed efficiency may hold the answer (Bottje and Carstens 2009; Kelly et al. 2011). Energetically inefficient or [+] RFI livestock are lower in muscle and liver mitochondrial respiration rate (Kolath et al. 2006), ADP-controlled oxidative phosphorylation (Carstens and Kerley 2009) and mitochondrial complex protein content (Kelly et al. 2011), and higher in mitochondrial derived reactive oxygen species production (Bottje and Carstens 2009), uncoupling protein 3 mRNA (UCP3 a trigger of mitochondrial proton leak in muscles; Ojano-Dirain et al. 2007; Kelly et al. 2011) and protein carbonyl level (Ojano-Dirain et al. 2007) compared with efficient or [−] RFI animals. Increased protein carbonyl levels are indicative of oxidation stress and, along with increased levels of reactive oxygen species and proton leakage, would result in greater protein oxidation and damage to DNA. These changes may alter cell-mediated immunity and cause inefficient dams and their offspring to be more susceptible to stressful conditions (van Eerden et al. 2004). Alternatively, the improved early life survival of progeny from [–] RFI mothers may be due to their improved feed efficiency resulting in more available nutrients and a better uterine environment compared with [+] RFI mothers. Despite the finding that a significant difference was observed in calf death loss between [–] and [+] RFI dams, more work is needed to verify these results since the numbers of calves that died were relatively small.

CONCLUSIONS

These results show that when RFI was adjusted for backfat thickness and feeding behaviour no differences were observed in pregnancy rate, calving pattern and productivity in beef heifers. However, if RFI is not adjusted for body fatness and feeding behaviour then selection for efficient heifers may contribute to reduced pregnancy rates. The two- to threefold increase in calf death loss observed for inefficient heifers requires further research to understand why the offspring from these heifers are more stress susceptible.

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